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GENETICS

# of YELLOW POPLAR

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This publication is one in a series on the genetics of important forest trees of North America being published by the Forest Service, U.S. Department of Agriculture, in cooperation with the Society of American Foresters. Development of this series is in accord with the resolutions of the World Consultation on Forest Genetics and Tree Improvement at Stockholm in 1963 and by the Fifth World Forestry Congress in Seattle, 1965. The Committee on Forest Tree Improvement of the Society of American Foresters undertook the preparation of manuscripts for North American species.

Genetics of Yellow-Poplar

James R. Wilcox[1] and Kingsley A. Taft, Jr.[2]

INTRODUCTION

The *Liriodendron* genus, a member of the Magnoliaceae family, includes two species: *L. tulipifera* L. (yellow-poplar, tulip-poplar, tulip-tree), found in the eastern half of North America, and *L. chinense* (Hemsl.) Sarg. native to Southeastern Asia. Yellow-poplar, because of its excellent form, rapid growth, and the exceptional working qualities of the wood, is considered one of the most important hardwood species in the United States.

Yellow-poplar grows throughout the Eastern United States from southern New England west through western New York and southernmost Ontario to southern Michigan, and extends south to Louisiana and Florida (fig. 2). Within this area it frequently occurs in pure even-aged stands on former old fields and cutover areas. In mixed stands it occurs with the oaks, gums, hickories, red maple, and in the southern part of its range with loblolly and shortleaf pine.

Successful seedling establishment requires mineral soil, adequate moisture, direct sunlight, and some shelter by a light cover of grasses, shrubs, or trees. Because yellow-poplar is intolerant to competition, overtopping, which would reduce height and diameter growth, must be avoided (Fowells 1965). The species makes its best growth on moderately moist sites with well-drained, loose-textured soils.

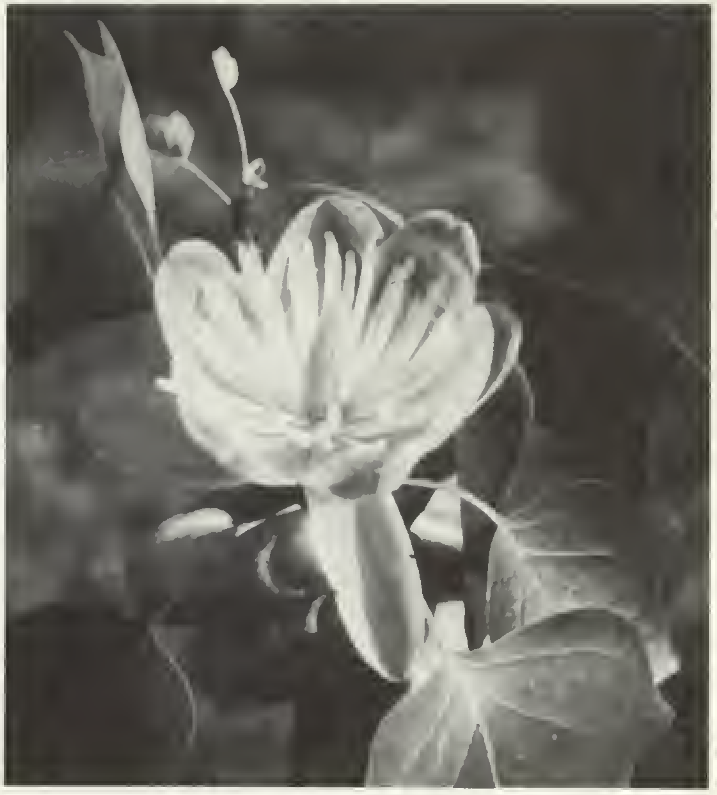

Figure 1. The large, showy blossom of the yellow-poplar lends itself to easy handling in pollination work.

SEXUAL REPRODUCTION

Reproductive Development

The flower of yellow-poplar is perfect, pedunculate, and cup shaped. It is surrounded by a sheath of imbricated, early deciduous sepals. The corolla is comprised of six petals, light green in color, each about 2 inches long, with an orange band at their base in which the nectaries are located. Adaxial to the petals are the stamens numbering 20 to 40. The gynoecium is located within the ring of stamens and consists of 60 to 100 pistils or carpels with one-celled ovary, a narrow, laterally flattened style, and a short recurved stigma (Sargent 1947).

Flowers usually begin to appear at about age 15, but grafts begin flower production in as few as 2 to 3 years (Thor 1965). The flower is large and showy and begins to open early in the spring but after the leaves are produced. On a given tree

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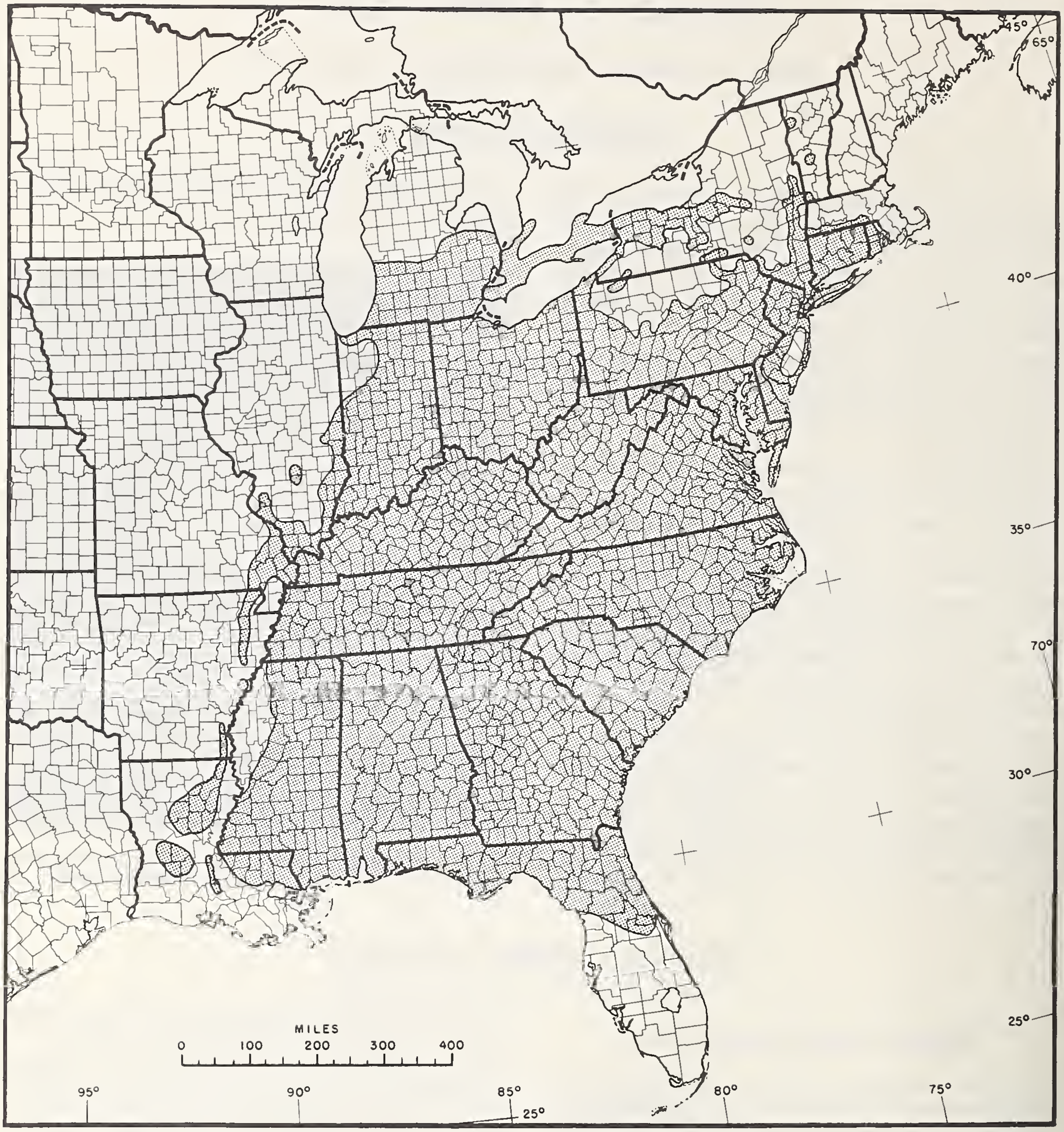

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Figure 2. The range of yellow-poplar.

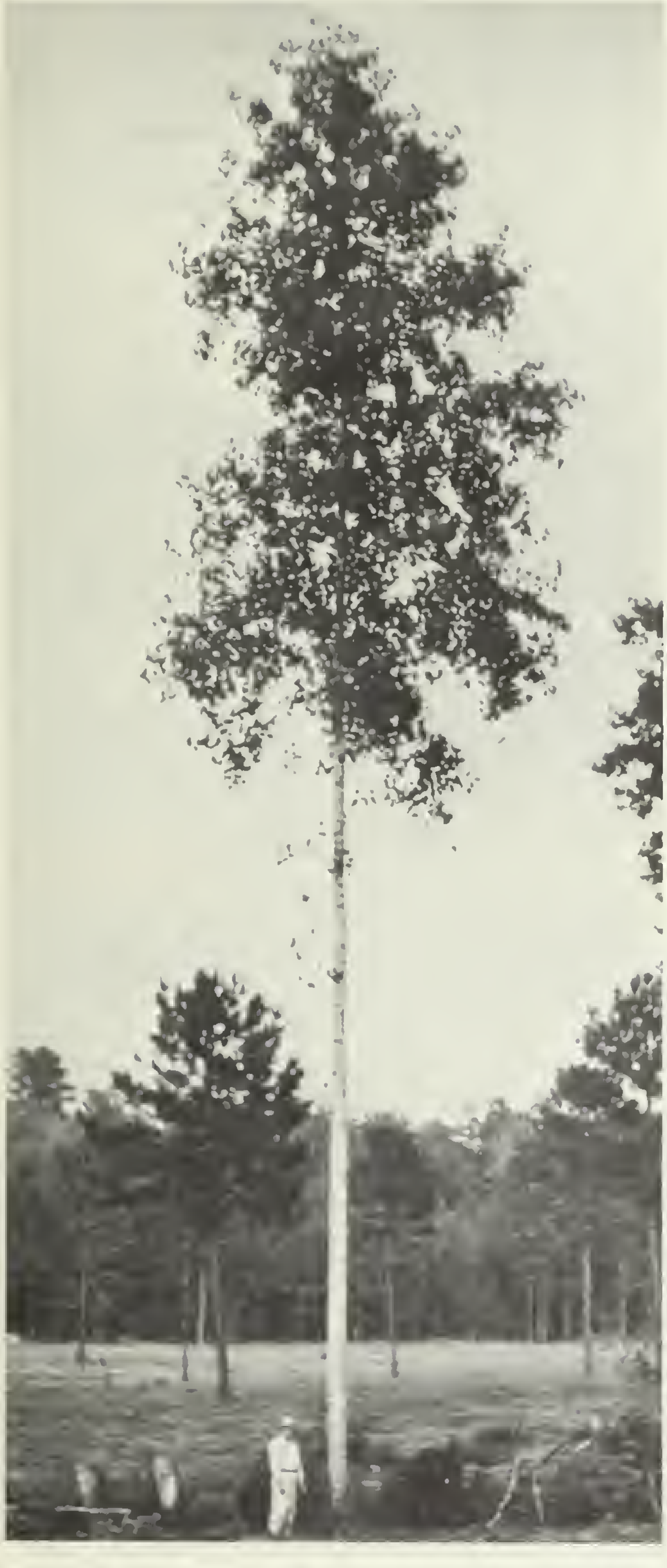

Figure 3. The straight, well-pruned trunk and narrow crown trunk are an outstanding feature of the yellow-poplar.

flowers will bloom for at least 2 weeks and sometimes as long as 6 weeks depending on the total number present. They are easily recognized by the large ovoid buds quite similar to that of the tulip.

Insects are the principal pollinating agents with yellow-poplar, in contrast to most commercially important species in which wind is the main pollinating factor. Flies, beetles, honeybees, and bumblebees in decreasing order of abundance were observed on opened flowers (Wright 1953).

The rank of the honeybee is very strongly related to whether domestic or wild hives are present, and if domestic, to whether they have been managed to take full advantage of the early, profuse yellow-poplar nectar flow. A beehive must produce two to three broods of young, each requiring about 3 weeks, before maximum strength is reached. Yellow-poplar usually blooms during the early hive building period, and thus the full effect of the honeybee is not felt. Under proper management, domestic hives can be given an early pollen supplement with which they can raise young and then be at full strength at flowering time (Taft 1962; Wolfe 1950). Additional hive management suggestions are given by Clarke 1956; Phillips and Demuth 1922.

The earliness of the yellow-poplar bloom and consequent weakness of most wild honeybee hives probably is a strong contributing factor to the usually low seed viability of the species. A second factor might be that insects tend to move from flower to flower within the crown of a single tree which would result in selfing. A third contributing factor to low seed viability is the very short receptivity period of each individual flower. Kaeiser and Boyce (1962a) found this to be 12 to 24 hours after the flower opens. When the stigmas have turned brown, the flower is no longer receptive.

Under natural conditions only about 10 percent of the samaras contain at least one filled seed. Based on two potential seeds per samara, this is only 5 percent viability. The development of the seed of yellow-poplar was first described by Maneval (1914), later by Guard (1943), and more recently by Boyce and Kaeiser (1961), and Kaeiser and Boyce (1962a). The latter authors concluded that insufficient insect pollination, the presence of self-incompatibility within a tree, and also incompatibility between adjacent trees are probably the main causes of low seed viability in this species.

Pollination Techniques

Controlled pollination work with yellow-poplar has been done by several workers (Carpenter and Guard 1950; Wright 1953; Taft 1962, 1966a, 1966b; Thor 1965; Sluder 1966; Stairs and Wilcox 1966). There were many similarities in the procedures used, also some differences.

Emasculation should be done just before the bud opens. At this time the bud is 1 to 2 inches long and one-half to 1 inch in diameter. It will be soft to the touch indicating that a space exists between the gyneocium and petals. Buds of this type are emasculated by removing the entire perianth and the stamens.

Either fresh or dried pollen can be used for each pollination. Taft (1962, 1966a) used fresh pollen by removing the flower petals at anthesis and using the dehiscing anthers, still attached to the receptacle, like a paint brush. Buds had to be collected shortly before they opened and kept in isolation until the anthers began to dehisce. This is particularly adaptable when flowers are abundant or when working in a seed orchard or pollinating trees which are located fairly close to each other.

However, if the time between anther dehiscence and pollination is great or long distances between parent trees exist, then pollen collection and drying may be necessary. Taft (1962), Stairs and Wilcox (1966), and Wilcox (1965), describe pollen preparation methods. Dried pollen should be diluted and can be applied with a fine brush. Sluder (1966) suggests extracting pollen in water and pollinating with an atomizer.

Since nearly opened buds are used for control pollinations, prebagging is not necessary. Bagging after pollination apparently should be done to avoid unwanted insect pollination. There is a possibility that post pollination bagging is not even necessary. Taft (1962) emasculated but did not pollinate or bag a large number of flowers. Because the species is parthenocarpic (Wright 1953) the fruit developed, but out of about 1,100 samaras no viable seed were observed. Boyce[3] confirmed this possibility. He selected a total of 200 groups of three adjacent flower buds on five yellow-poplar trees. In each group one bud was emasculated by removal of perianth and stamens but not pollinated; a second bud was emasculated and pollinated; and the third bud was left to open and be pollinated naturally. Table 1 gives the results.

Apparently, removal of the perianth and stamens almost eliminates insect pollination. Bagging after control pollinating is not necessary if one is willing to accept a very low percentage of unidentified pollinations.

Another control pollination technique is described by Sluder (1966). His method involves shooting down large branches from mature trees and grafting flower buds to seedling rootstocks. Control pollinations are then made on these grafts. However, after this first growing season, it may be several years before another flower appears.

Table 1.—*Results of pollination tests of 200 groups of three adjacent flower buds on five yellow-poplar trees*

Type of treatment	Number of samaras examined	Number of filled seed
Perianth and stamens removed, pistils not pollinated	14, 720	[1] 7
Perianth and stamens removed, pistils cross-pollinated	13, 840	4, 152
Buds permitted to open naturally and be insect pollinated	15, 528	1, 552

[1] Four filled seed occurred in 1 cone, 2 in 1 cone, and 1 in another cone.

Results of control pollinations, both cross and self, are reviewed by Thor (1965). It is apparent that considerable variation exists due to the different pollination techniques; however, there are some unexplained portions probably due to genetic incompatibilities both within and between trees (Taft 1966b; Boyce and Kaeiser 1961).

Seed Handling

Seed production is generally good from year to year on a given tree; however, much of it may be parthenocarpic. As previously mentioned the viability of seed averages only about 10 percent. This viability may be affected by position of the cone in the tree or position of the seed within the cone (Wean and Guard 1940; Guard and Wean 1941; Carvell and Korstian 1955).

The seed fall in October and November with the greatest amount occurring during periods of high temperatures and low rainfall (Carvell and Korstian 1955). Seed fall densities as high as 300,000 to 500,000 per acre are found directly beneath a good seed tree (Engle 1960).

Seed can be collected by climbing the tree and picking individual cones or by spreading a canvas or sheet under the tree to catch the seed as they fall. Collection from recently felled trees is a third possibility (TVA 1940). A quick check on the percentage of filled seed can be made by cutting laterally across a few cones from a potential collection tree. This will expose about a dozen seeds. If with every cut two or more filled seeds are exposed, then the seed of that tree should be average or better.

The large tree-to-tree variation in viable seed requires accurate testing methods so that the number of filled seed can be determined and thus better control over seedbed density obtained. This is even more pertinent when valuable seed such as that from crosses or selfs are to be evaluated. Cutting tests are destructive and usually not enough seed are available for a germination test. Kaeiser and Boyce (1962b) proposed the use of X-ray photography to separate filled and empty seeds. Taft (1962) further tested the technique and found a significant correlation (r—0.990) between the number of filled seed as shown in an X-ray and the number of seed that germinated in greenhouse flats. Under the less controlled conditions in the nursery only 75 percent of the filled seed germinated (Taft 1966a).

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[3] Personal communication with S. G. Boyce.

Seed storage, germination, and yellow-poplar nursery practices are covered in the Woody-Plant Seed Manual (USDA 1948). However, a few additional comments are in order. Maximum viability can be maintained for several years by storing the seed dry at temperatures just above freezing. Moist seed will also retain its viability for a limited number of years. Clark and Boyce (1964) found that seed do not lose their viability after four winters in forest litter. They also found that complete germination is not accomplished in 1 year of stratification; some germination occurs the second year after sowing. Therefore, stratified seed may be stored for several winters (Paton 1945). Paton also proposed stratifying seed by burying it in layers of moist sand. The same effect can be accomplished by soaking the seed 3 to 4 days, placing in a polyethylene bag and storing at about 35° F. It should be possible to store the seed this way at least 2 years and possibly longer.

ASEXUAL REPRODUCTION

The current approach in most tree improvement programs is selection. This implies some type of vegetative reproduction, either grafting or rooting to retain the genotype of the selections.

Rooting

Rooting, by far the least expensive asexual reproduction method has, until recently, been the most difficult. Enright (1957) reports on some early attempts and also describes a successful rooting method. Very high auxin concentrations are used on summer cuttings with greatest success at 20 mg./ml. in sand and soil. Extremely valuable seedling material can be multiplied by splitting the seedling (Nelson 1957).

The first major breakthrough in yellow-poplar rooting was made by McAlpine (1964). By using cuttings taken from stump sprouts he was able to obtain about 70 percent rooting. He found that the juvenile condition of these stump sprouts was probably the most influential factor in rooting and in their ability to be successfully transplanted. Further proof of the importance of juvenility was found by Kormanik and Porterfield (1966). They were able to stimulate epicormic branch development on older trees and then root these juvenile branches.

Grafting

Almost all grafting methods can be used on yellow-poplar with some success. Scions can be collected as early as December and stored in wet sphagnum moss at 35–40° F. until grafting time (Hatmaker and Taft 1966). Seedlings ranging in age from 1–0 bare-rooted seedlings to 4-year-old stock trees can be used as rootstocks. In addition, budding can be done in August.

Bench grafting is probably the easiest and most economical grafting method. Scions are grafted to bare-rooted 1–0 seedlings indoors during February or March. The whip graft is tied with raffia (instead of a rubber band) and the scion and graft union are completely painted with grafting wax. Completed grafts are stored in wet sphagnum moss until early spring when they are lined out. Each graft is planted with the graft union and part of the scion covered and packed with soil. Irrigation immediately after planting and a few weeks thereafter is essential. Once the graft has taken and begins to grow the raffia tie will disintegrate (Hatmaker and Taft 1966).

When 1–1 rootstocks are available either the whip graft or side graft is used depending on rootstock size. Again, both the graft union and scion are painted with grafting wax. In general, the longer a graft union has a chance to form before active scion growth, the better. If a terminal bud is present on the scion it should be removed. This will result in a 6 to 10 day delay in scion growth initiation. No polyethylene or paper bag protection of the graft is needed.

The side graft is particularly adaptable when the rootstock is quite large (Churchwell 1965). If sufficient scionwood is available two or three grafts can be made per rootstock to insure success of at least one. Usually the top of the rootstock is not removed until the scion begins to grow. Sprouts on the rootstock should be trimmed several times during the growing season.

Budding is another vegetative propagation technique and is usually done during late summer when the sap is moving (Funk 1962). Either chip or patch budding can be used. The important point is that the bud not break dormancy until the following spring. This can be prevented naturally if the top of the rootstock is not removed until April or May (Hatmaker and Taft 1966).

GENETICS AND BREEDING

Natural Variation

Growth. Within the natural range of yellow-poplar, length of the growing season varies considerably. Kramer (1943) found that although yellow-poplar growing in North Carolina had a longer growing season than in New England, the seasonal course of growth was the same in both areas. Growth began in the spring before danger of frost had past but ceased long before the first autumn frost. Spring frost damage to yellow-poplar has been reported (Funk 1958; White and Finn 1964) and varies by seed source and site. In North Carolina yellow-poplar was somewhat unique among the tree species studied in that it had no peak month for growth but grew about the same every month from April to July and finally ceased in September, utilizing more of the growing season than the other species.

There is good evidence that growth initiation in the spring and cessation in the fall is strongly influenced by photoperiod (Garner and Allard 1923; Kramer 1936). Zahner (1955) demonstrated that length of the dark period was critical for yellow-poplar since trees growing on a cycle of 9.5 hours of light and 14.5 hours of dark made less than half the height growth as trees on the same cycle, except for a ½-hour light interruption at the middle of the dark period. Downs and Borthwick (1956) considered the critical photoperiod (photoperiod required to maintain vegetative growth) to be 16 hours for yellow-poplar.

Specific gravity. Individual yellow-poplar trees vary considerably in specific gravity and rapid genetic improvement should be made by selection for this character. Thorbjornsen (1961) evaluated wood properties of 63 trees from 10 stands in each Tennessee and southeast Kentucky. Most of the variation in wood density was associated with individual trees (70 percent) relative to that within trees or among stands. Density at 5 years was strongly associated with density at 25 years ($r=0.73$). Taylor (1964) observed little variation in specific gravity among three physiographic areas in North Carolina: Coastal Plain, Piedmont, and Mountain. However, large variations were observed among trees in each of two 16-tree plots within each area. Trees with high average specific gravity generally had higher values at all sampling points than trees with low specific gravity. These same patterns of variation for this character have been confirmed by Kellison (1967).

To determine the pattern of variation in factors contributing to wood density, Taylor (1964) evaluated vessel volume, ray volume, and fiber wall thickness of yellow-poplar. Statistically significant differences were found among trees within stands for both ray volume and fiber wall thickness, but not for vessel volume. Specific gravity, however, was correlated with both vessel volume and fiber-wall thickness.

Extractives have not been found in sufficient amounts to appreciably influence specific gravity determination of yellow-poplar (Thorbjornsen 1961; Taylor 1964).

Fiber length. In contrast to the above results, Thorbjornsen (1961) found most of the variation in fiber length of yellow-poplar was within trees compared to that associated with individual trees or stands. Taylor (1963) reported a linear increase in fiber length of about 1/3 mm. from the earliest formed springwood through the last formed summerwood. He advocated making comparisons among trees from constant points within annual rings to reduce the within tree fiber length variation. Utilizing this technique he found fairly large differences among individual trees within physiographic areas of North Carolina (Taylor 1964).

Branch angle. Kellison (1967) obtained a good estimate of yellow-poplar branch angle by measuring six consecutive major branches down the bole starting from a point approximately one-third distance from the crown apex. He found significant differences between trees within stands (0.01) and between stands within areas (0.05) but no differences between either areas or physiographic regions in North Carolina for this character.

Leaf, fruit, and seed characteristics. Detailed measurements of yellow-poplar leaves were summarized by two linear measurements and five ratios by Kellison (1967). All foliage properties but one differed significantly (0.01) between positions within trees, between trees within stands and between areas within physiographic regions of North Carolina. He concluded that the ratio of leaf width to length was suitable for differentiating foliage characteristics of the species.

Consistently large differences were found between individual trees for cone length, number of seeds per cone, samara length and samara width (Kellison 1967). There was a tendency for the mountain areas to have larger cones, a greater number of seeds per cone, and larger samaras than either the Piedmont or Coastal Plain region.

Provenance Studies

Provenance studies evaluate the performance of germ plasm from several different sources in a common environment, thus inherent differences between sources can be observed. In a plantation near Charleston, S.C., trees from a Coastal Plain source in eastern North Carolina averaged almost twice as tall (4.4 vs. 7.9 feet) in the third growing season as those from a mountain source in western North Carolina (Lotti 1955).

In a test near Asheville, N.C., Sluder (1960) evaluated seedlings from 16 geographic sources ranging from north-central Mississippi to Michigan and New York. Although average total heights differed significantly between sources after one growing season, there were no differences between sources after five or 10 growing seaons.[4] Average 10-year height for each source was highly correlated with 5-year heights ($r^2=0.9016$). After 5 years, seedlings from the local source had better survival than those from several other locations; however, no geographic trends were apparent for this character. Date of growth initiation was correlated with length of the growing season ($r=0.900$), date of the last killing frost ($r=0.808$), and latitude ($r=0.575$) at the source. Date of height growth cessation was significantly correlated with date of the first killing frost at the seed source ($r=0.518$).

Funk (1958) reported that damage from a spring frost in a 3-year-old yellow-poplar plantation in Ohio was generally related to latitude of the seed source. Trees from the four southernmost locations suffered more extensive dieback than those from three more northern sources.

In a study of four geographic sources of yellow-poplar ranging from central Mississippi to Sewanee, Tenn., differences in 6-year height were not statistically significant over all test locations (Farmer, Russell, and Krinard 1967). At certain test locations some southern sources were significantly taller than some northern sources. Trees from southern sources foliated earlier than those from more northern areas.

The existence of photoperiodic ecotypes of yellow-poplar has been demonstrated by Vaartaja (1961). Under very long days (3-hour dark periods) the northernmost source (Michigan) grew best and the southernmost source (Georgia) was poorest. With dark periods from 6 to 12 hours, the converse was true. The Indiana source was intermediate in growth at all photoperiods.

Several studies have reported significant differences between seed sources and individual trees within sources in seed quality and seedling height. Perry and Coover (1933) noted great variation in the number of sound embryos among individual trees. Average height of 1 year seedlings differed significantly between individual seed trees within as well as between sources (Limstrom and Finn 1956). Variation between heights of seedlings from a single tree were often greater than mean differences in heights of progenies between seed trees and sources. Similar results have been subsequently reported by Limstrom (1959).

These data on seed quality and seedling height differences must be interpreted with caution since they may reflect differences in the extent of cross- versus self-pollinated seeds from different trees rather than inherent superiority of parent trees or sources (Limstrom and Finn 1956; Sluder 1964).

Many of the seed source studies established to date are limited either by the range of sources tested or the number of locations where sources have been evaluated. More comprehensive tests are needed across the southern and northern range of the species. Within each of these areas outplantings should be made at several locations to assess more accurately the effects of provenance on growth and cold tolerance.

Genetic Analyses

Data from controlled crosses remove the possible bias of differential cross- versus self-pollination from open-pollinated progeny tests and provides more accurate genetic information. Carpenter and Guard (1950) compared seed yields and early height growth from self-, cross-, and open-pollinated seed of trees in Tippecanoe County, Ind. The percentage of filled seed from individual trees was consistently higher for cross-pollinations (28 to 90 percent) than for either open- (2.4 to 34.8 percent) or self-pollinations (0 to 5.6 percent). In spite of wide variations in the size of both open- and cross-pollinated seedlings, the average total height after 4 months of growth was consistently higher for the crosses than for open-pollinated seedlings. Reciprocal crosses gave almost uniform increases in vigor. Pollen from more distant trees produced the greatest increase in vigor. These limited data indicate that excellent opportunities exist to exploit heterosis for growth in progenies from crosses among parents from different stands.

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[4] Sluder, Earl R. 1967. Seed source study of yellow-poplar. Unpublished Progress Report. Southeastern Forest Experiment Station, Asheville, N.C.

Three yellow-poplar trees from south Mississippi were crossed with each of three trees in central New York by Stairs and Wilcox (1966). Seed germination values for controlled pollinations were 31 percent compared with a mean germination of 9 percent for open-pollinated seed. After 200 days, height growth of the crossed progenies (75.7 mm.) was significantly superior to that of the open-pollinated progenies (44.8 mm.).

Taft (1966a) evaluated progenies from open-, self-, and diallel cross-pollinations among 13 yellow-poplar trees in North Carolina. The average percentage of filled samaras from crosses (14.7 percent) exceeded those from selfs (3.5 percent) and open-pollinated (6.3 percent) progenies. A comparison of percentage filled samaras from cross-pollinations revealed a tremendous amount of variation in cross compatibilities among the parent trees. Although a higher proportion of the filled seed germinated from crosses (94 percent) than from selfs (79 percent), the germination rate of the different kinds of progenies did not differ. A greater proportion of the crossed and open pollinated progenies than of the selfed progenies survived the first growing season and were taller at the end of 1 year.

Of the leaf measurements evaluated, only the ratio of length to width of parent trees and their self- and cross-pollinated families were significantly related. All ratios compared among various leaf measurements were strongly related between crosses and selfs from the same parent tree, indicating the progeny of a particular tree have a characteristic leaf shape.

Data were reported by Taft (1966a) on the diallel analyses involving progenies from eight of the parent trees. Estimated additive and dominance components indicated complete dominance or overdominance for first year height, assuming gene frequencies of 0.5 to 0.75. From analyses of height during the first growing season, Taft concluded that total height differences between progenies were not due to differences in growth rate *per se* but in differences in time of growth cessation. The ratio of leaf length to width was controlled primarily by additive genes.

Whether or not unrelated trees from widely separated stands have different genes affecting tree form is unknown. If so, crosses between trees of superior form from different areas may exhibit heterosis for growth but may regress in form. Interrelationships between growth and form, therefore, should be evaluated in such crosses. Studies have been initiated to evaluate progenies from crosses among trees within stands, between stands within the same region, and from different regions, which will be pertinent to this problem (Thor 1966; Wilcox and Stairs[5]).

Cytogenetics

Yellow-poplar is considered to be a diploid with 19 pairs of chromosomes. The average chiasma frequency per bivalent of 1.14 is within the range reported for other species of the Magnolias (1.06 to 1.17) (Whitaker 1933). No evidence of chromosomal or meiotic irregularities have been observed (Boyce 1959). In a cytogenetic comparison between *L. tulipifera* and *L. chinense* Parrish (1957) was unable to demonstrate any morphological distinction between the chromosome complements of the two species. The chromosome complement of *L. tulipifera* consists of four chromosomes with median, 13 with submedian and two with subterminal centromeres.

IMPROVEMENT PROGRAMS

Objectives in a tree improvement program must be related to utilization of the species. Where yellow-poplar is to be grown for lumber and veneer, a high proportion of the trees must have the potential for utilization in these high value products. Where pulpwood is the major objective, increased emphasis should be put on maximizing wood production per unit of land rather than on the individual tree. Specific objectives, therefore, may vary with different wood utilizing industries. The following general procedures are suggested for the genetic improvement of yellow-poplar.

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[5] Intraspecific hybridization in yellow-poplar. Unpublished cooperative study, Institute of Forest Genetics, Gulfport, Miss., and College of Forestry, Syracuse University, N.Y.

Selection of Stands

Stands of yellow-poplar should be selected in the same climatic zones where the trees are to be grown. Early results of seed source studies have not shown appreciable differences in growth among provenances. However, southern provenances have shown greater susceptibility to frost damage which could affect tree form. Limstrom (1965) and Rudolf (1956) have set up seed collection zones for the Central States based on climatic and geographic conditions considered critical in limiting the distribution and planting range of tree species. These should be used as guides in this area.

Since yellow-poplar occurs in southern mountains as well as lowlands, stands should be selected where the climate is analagous to that where trees will be grown rather than on the basis of latitude only.

Within these areas stands with a high proportion of vigorous, well-formed trees will offer the best opportunities for critical selections.

Selection of Trees for Clonal Orchards

Primary consideration should be given to individual trees rather than to stands. However, the number of trees selected per stand must be restricted because of incompatibility among related trees resulting in low seed viability. Ideally only one tree should be selected per stand. Where numerous high quality trees are available in a single stand, one or two additional selections could be made if these are dispersed in the clonal orchard.

Criteria for selecting trees for inclusion in an improvement program have been reviewed by Limstrom (1965). Emphasis here will be on priority of specific characteristics.

Form. Individual tree selection should be based primarily on form since the value of yellow-poplar logs will be dependent upon quality as well as size. High standards should be adhered to in selecting straight trees with minimum sweep or crook.

Forks limit the length of log which can be cut for lumber or veneer. Yellow-poplar is characteristically free of forks and only those trees should be selected which have a single stem for at least 80 percent of their height.

Taper and bole symmetry also contribute to tree form. Since taper is strongly influenced by site, comparison should be made between select trees and others on the same site for minimum taper. Symmetrical boles are desirable in veneer bolts and contain less tension wood than asymmetrical ones. Very high standards should be retained in selecting symmetrical stems.

Defects. Yellow-poplar lumber is manufactured into products cut from clear wood between defects; therefore, the kind and distribution of defects largely determine the value of an individual tree and its products. Freedom from defects should receive equal priority with tree form in selection standards.

Individuals with small branches which prune at an early age should be selected, since large branches persist on the tree leaving knots extending out into the wood.

Epicormic sprouts can cause severe defects in yellow-poplar. Wahlenberg (1950) reported that naturally heavy sprouters tended to become progressively worse with release cutting. Resistance to sprouting will be particularly important in plantations established at high densities where pulpwood release cuts will be made prior to the final harvest. Selections for use in an improvement program should be completely free of epicormic sprouts. Intensive selection for this character may be particularly profitable in stands where release cuts have been made in recent years.

Defects may also be due to injury by disease or insects. Selections should be free from apparent injury by such pests.

Growth rate. Secondary consideration should be given to growth, but only dominant or codominant trees should be selected in a stand. It is anticipated that specific parental combinations will result in rapidly growing progenies; good growth can be attained more effectively this way than by selection for the largest parent trees.

Where yellow-poplar is to be planted for pulpwood, emphasis on growth may take priority over characteristics affecting tree form or causing defects since volume of wood production is the primary objective.

Specific gravity. Since strength values of yellow-poplar wood are correlated rather closely with specific gravity (Luxford and Wood 1944) selection for this character will depend upon desired weight and strength of the wood. Higher densities result in more pulp per volume of wood; therefore, increasing specific gravity would be a desirable objective in yellow-poplar grown for pulping. The pattern of variation for this character indicates that rapid progress could be made in changing specific gravity to be a desired level. Priority given to specific gravity compared to other characteristics will depend upon the purpose of the plantation, and will vary with wood-using industries.

Fiber length. There appears to be little inherent variation for fiber length in yellow-poplar; hence, changing this character by selection would be a slow process. Rapid strides in utilizing hardwood fibers by the pulping industry in recent years indicates that technology could be modified to make use of existing fiber properties more efficiently than attempting to change them through breeding. Fiber length, therefore, should be ignored when making selections.

Seed Orchards

Yellow-poplar is ideally suited to improvement in clonal seed orchards. Parents with the ability to combine to produce vigorous, well-formed progeny can be identified and maintained as clones.

Seedling seed orchards would not be effective for yellow-poplar improvement. Because of specific parental compatibilities, such an orchard would be worthless as a progeny test unless control-pollinated progenies were used. Even then, individual trees in the orchard would have to be retested for combining ability before they were retained or discarded.

Recent research has opened up the possibility of combining test crosses with clonal orchard establishment. Utilizing the techniques of Sluder (1966), scion wood bearing flower buds could be collected from selected trees and grafted onto potted rootstocks. Crosses could be made among the clones to identify parents with good combining ability. On the basis of seed yields (compatibility), the grafted rootstocks could be planted in the clonal orchard in an arrangement to insure unrelated, compatible trees in close proximity. If all crosses cannot be made on the potted rootstocks, some may have to await first flowering in the orchard.

As soon as progeny tests from the initial crosses identify trees with good specific combining ability, additional material from good combiners can be top-worked onto the original rootstock. Since bees tend to move from flower to flower on the same tree, this could insure maximum seed yields from the best parental combinations.

Intensive orchard management will be particularly important with yellow-poplar. Because of the incompatibility system in this species, techniques must be developed to insure adequate cross-pollination in the orchard. The possibility of grafting more than one parent clone onto a single rootstock should be fully explored. Certain grafts may tend to outgrow others and careful pruning may be required to equalize scion development. The placement of colonies of bees in the orchard and the strain of bees used may influence how effectively they work to insure adequate cross-pollination. The effects of fertilization, cultivation, and pruning on flowering and subsequent seed set should be determined.

Nursery Evaluation

There is a good evidence that premium seedlings in the nursery consistently increase their growth advantage over poorer seedlings for at least 8 to 10 years (Funk 1964). Nursery selection or grading should be an integral part of the improvement program.

Seed from the clonal orchard would be grown in the nursery for 1 year and released as 1–0 planting stock. Some seedlings would be from self-pollinations, some from cross-pollinations of poor combining ability, but hopefully most would be from cross-pollinated seed of good combining ability. Nursery stock would be graded to eliminate the smaller seedlings, the selfs or progenies of poorer crosses. Absolute uniformity of nursery beds would be required to minimize environmental effects and maximize genetic differences for growth among the progenies.

Interspecific hybrids, polyploidy, mutation breeding, or selfing followed by selection and hybridization offer possibilities of contributing to yellow-poplar improvement in the more distant future. At present, research emphasis should be put on problems which will result in the most rapid immediate improvement of the species.

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1969. Genetics of Yellow-poplar (*Liriodendron*). USDA Forest Serv. Res. Pap. WO-6, 12 p.

Characteristics of yellow-poplar including reproductive development, pollination techniques, seed handling, rooting and grafting, cytogenetics, natural variation, provenance, and genetic studies are reviewed as they apply to the genetic improvement of the species. A breeding system including tree selection criteria and clonal seed orchard establishment and management is suggested.

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